

Anser ruficollis. Only one of these very rare birds was observed.

Cygnus musicus. Very common.

Anas tadorna.

A. boschas.

A. strepera.

A. acuta.

A. penelope.

A. crecca.

A. clypeata.

A. nyroca.

A. ferina.

A. clangula.

Common. Wild fowl are most abundant throughout Macedonia, and had I made a longer stay in the country, no doubt many other species would have been observed besides those mentioned.

Mergus serrator. Common.

M. albellus. Very numerous, though none but females were observed; the same remark applies to the Ionian Islands. Might not some of these supposed females have been males, not having assumed the breeding plumage?

Pelecanus onocrotalus. Very common.

Carbo cormoranus. } Common.

C. graculus.

C. pygmaeus. Most numerous.

III.—Observations on the Cell-Membrane of Plants.

By G. H. K. THWAITES*.

IF a decaying vegetable organism is brought before us, in which nothing remains of the former structure but the cell-walls, it is difficult to conceive that this skeleton, as it were, has performed an important part in the vital processes of the plant,—that it has been an agent in the chemical changes which had been going on during the processes of secretion, assimilation, &c.,—in fact, that it has been any other than a mere skeleton for the support of the important parts of the organism: I say that, divesting the mind of preconceived notions respecting the functions of cell-membrane, it is difficult to regard it, under such circumstances, otherwise than in the light I have just mentioned. I hope to be able to show that this is really the view which should be taken of it.

To prevent any misconception of my meaning, I will just state that when using the term “*endochrome*” in the succeeding part of my paper, I wish it to be considered as comprising the entire contents of the cell, including the nucleus or nuclei. The terms *cell-membrane* or *cell-wall* explain themselves.

There cannot be a more satisfactory way of showing the subordinate character of the cell-membrane than by exhibiting a perfect living organism in which it does not exist, and there are

* Being the substance of a paper read at a Meeting of the Bristol Microscopical Society, April 8, 1846.

some plants, belonging to the family *Oscillatoria*, in one of which (a species of *Spirulina*) there appears to be no real membrane—the plant consisting of a mucous matrix, out of which, when the species is mature, emerge oscillating spiral filaments, which from their exhibiting no trace of cell-membrane, or even of any division, by *septa*, into separate portions, and from the rapidity with which they become decomposed, I believe to be continuous masses of endochrome held together by mucus. Another species to which I would direct attention is the *Lyngbya ferruginea*, Agardh, a plant scarcely differing from *Oscillatoria*, except in the greater firmness of the membranous sheath which invests each filament: the filaments of this plant are composed of lenticular masses of endochrome, and during the early part of their growth are inclosed in a membranous sheath; from this, however, they emerge when mature, and soon afterwards become broken up into the separate masses of endochrome, each of which appears to be held together by a kind of mucus, and not to be surrounded by a cell-membrane. I am inclined to believe that the *Oscillatoria* generally have no real cell-membrane, unless the common sheath, investing each filament, be considered as such. In *Microcoleus*, one of the same family, the filaments are invested with a *mucous* or *gelatinous*, not *membranous* sheath; proving that the membranous sheath which incloses the filaments of the above-named *Lyngbya* is not to be viewed in the light of the ordinary cell-membrane, though its functions are probably identical with it.

When treating of such objects as the foregoing, I am aware of the danger of advancing a negative proposition; of stating that certain structures do not exist, when an improved method of observation may eventually discover their presence: I would therefore request that what has been just advanced may be considered as what I firmly believe to be the case, and not as an absolute indisputable certainty. But the doctrine I would advance does not rest solely upon the possibility of proving the absence of cell-membrane in a perfect organism; though it would naturally derive weight and probability from such a source.

I now proceed to point out instances in which the cell-membrane is seen to be of quite a secondary character; and that its development is regulated entirely by the condition of the endochrome it contains, and that, in fact, it owes its existence to this endochrome. The production of cell-membrane and endochrome has the appearance frequently of being synchronous, but the endochrome may sometimes be seen becoming invested with a cell-membrane, and this may be well-observed during the formation of the spore of *Zygnema* and other species of *Conjugateæ*. Those who have paid attention to this family of plants are well aware, that previously to the formation of the fruit, two cells unite by

means of a short tube developed from each, and through the canal formed by the union of these the endochrome of one of the cells passes into the other cell, becomes mixed with its endochrome, and subsequently around this mixed endochrome a cell-membrane is developed. This membrane would certainly appear to be developed by the endochrome and not by one of the original cell-walls, otherwise we could not expect it to be entirely influenced as to its form and size by the contained endochrome, but that there would be indications of its being independent of this. The spore-membrane, however, not only corresponds in extent with the contained endochrome, but if, as is sometimes accidentally the case, the mass of endochrome has become divided into two portions, each of these portions becomes covered with a cell-membrane; thus showing that the relation is between these, and not between either and the original cell-wall. That a *spore* of *Zygnema* represents a cell of the same plant is well-shown by the mode of fructification of an allied genus, *Vesiculifera*, where it is evident that such is its character (see p. 333).

Amongst the Algæ the number of cells is often very much increased by fissiparous division; that is to say, a single cell becomes divided into two (sometimes four): the way in which this takes place is interesting, and I think throws light upon the ordinary production of cells. The process of the fissiparous division of cells may be well-seen in the large species of *Zygnema*; in these the endochrome is arranged in one or more spiral coils within the cell. When the latter is about to become divided, a slight disturbance of the regularity of the spirals may be observed just in that part of the cell where the division will take place; their continuity is subsequently broken at this spot, and soon afterwards the original cell may be seen to have become converted into two, with no apparent disturbance of the endochrome except just at the point where separation took place. [The large nucleus has also become divided into two.] Various explanations have been given of the mode in which the division of the cell takes place, but I believe the correct one is to consider that each half-endochrome develops around it a new cell-membrane—the old one remaining or becoming absorbed. I have certainly seen traces of the original cell-membrane in a fragile species of *Zygnema* found in this neighbourhood. In *Isthmia*, *Meloseira* and other genera which possess a siliceous cell-wall, it is distinctly seen that two perfect cells are developed within the original one, and this would lead us to expect the same thing to occur in all species where this mode of division obtains.

We may now proceed to the consideration of the ordinary mode of development of cells, and there is perhaps scarcely a species in which this can be studied to greater advantage than in the very

common *Conferva glomerata*. In this species the cells are extremely large, and the endochrome is in considerable quantity; and the cells apparently continue increasing in size during the whole period of their vitality, so that those at the base of the plant are larger than those recently developed. Some species of *Conferva* consist only of single unbranched filaments, so that, in these, new cells are added only at one point; but in the species under consideration new cells originate from every part of the plant, and thus we have a favourable opportunity of observing what takes place when a new cell is being produced from one which has been some time developed. A slight protuberance is observed upon the cell-membrane, which has the appearance of being caused by the enlarged contained endochrome endeavouring to force its way out of the cell. This protuberance increases at the same time with an increase of the endochrome, and becomes of some considerable length before there is any appearance of a septum dividing it from the original cell. The endochrome, however, subsequently divides, and a membrane is developed over each of the divided ends; or, what is the probable explanation, a development of cell-membrane has been taking place during the whole process, and, still going on, a membrane is now naturally formed over those ends of the endochrome where the previous continuity has been broken. That an addition is continually being made to the cell-wall is evident, since there is no other way of accounting for the increasing size of the cell and thickness of its membrane.

An abnormal growth which sometimes takes place in the cells or long tubes of *Vaucheria* will serve well to illustrate how immediately an increased production of cell-membrane is consequent upon an additional development of endochrome. The cells of *Vaucheria* are occasionally found to be infested with a species of *Vorticella*, an infusory animalcule. This little animal is seen occupying large pear-shaped protuberances upon the frond of *Vaucheria*, in which it deposits its ova. Now it is interesting to observe the mode in which these peculiar protuberances are formed. The *Vorticella* may, in some instances, be seen within the tube of the plant, and from the slight alteration in the endochrome, it may be inferred that the little animal has not been long present there; in other cases it may be observed that the presence of the *Vorticella* has caused an evident dilatation of the cylinder of endochrome with a corresponding enlargement of the cell-membrane; whilst in other examples this dilatation has gone on so as to have produced a large pear-shaped appendage to the frond, within which the *Vorticella* may be seen moving. But what I would wish particularly to draw attention to is the fact that the stimulus arising from the presence of the *Vorticella* has

been operating immediately upon the internal surface of the cylinder of endochrome, causing an abnormal development of this, accompanying and consequent upon which has been a corresponding and regular development of cell-membrane; showing that the amount of production of cell-membrane is regulated by the growth of the endochrome.

I will now proceed to make a few remarks upon a structure which is developed in greater or less amount in most Algae,—external to the cell-membrane,—possessing some characters in common with it, and probably in many cases performing a similar office in the œconomy of the organism. The structure I allude to is the *mucus* which surrounds the cells of Algae, and in some species, such as in many of the *Palmelleæ*, of considerable extent, so as to make up by far the greater part of the plant. In some of the *Palmelleæ* indeed, the plant at first sight appears to be composed of an amorphous gelatinous mass, containing cells imbedded in it, and would lead to the idea that this gelatinous mass is the matrix from which the cells are developed, and to which they owe their origin; but such is really not the fact. There are some species of *Palmelleæ* which show the character of this mucus very clearly, and in which its development can be traced without difficulty. In *Coccochloris cystifera*, Hassall, a species not uncommon in the neighbourhood of Bristol on rocks and walls, may be readily observed the circumstances under which the mucus is developed, and that this mucus is of definite form and quantity. This species of Alga, like most if not all the *Palmelleæ*, increases not only by an enlargement of its cells and the ordinary reproduction of these from a parent cell or spore, but during the development of the plant the number of cells is very much increased by fissiparous division—each cell becoming divided into two or four—no doubt in the same way as occurs in *Zygnema*, *Isthmia*, &c. Now if the plant, in which this process is going on, be carefully examined, it will be seen that the mucus is developed in definite quantity around each cell and doubtless by it. For we may perceive *one* cell in which there is no indication of fissiparous division; *another* in which this process has just taken place, but the cells are yet in close apposition; *another* in which the two new cells are separated to some distance from each other; and if we examine into what has led to their separation, we may find that this arises from a definite development of mucus around each of them and within the mucous envelope of the original cell; and *lastly*, we may find a pair of new cells of nearly equal size with the original one, each with nearly the ordinary amount of gelatine or mucus surrounding it, and the mucous sheath of the original cell nearly absorbed. In a *Palmella* found in Sussex by Mr. Jenner and sent me by Mr. Ralfs under the name of *P. hya-*

lina, the original mucous sheath appears not to be absorbed, but to be ruptured upon the production of new ones within it. Each cell of some species of this family is surrounded by two or more distinct mucous envelopes; and in some species a cluster of cells is also surrounded by a common mucous sheath, which is no doubt also developed from the cells. In other species of the *Palmelleæ* the cells are raised upon mucous prolongations caused by the development of mucus on one side of the cell. The curved moniliform filaments of the genus *Nostoc* would at first sight appear to grow in a mass of gelatine without any definite arrangement; but when, as is sometimes the case, the plant occurs with a single straight filament, this is found to be surrounded by a gelatine or mucus of definite diameter, showing that in this genus the amount of gelatine depends upon the number of cells. That the gelatinous stipes of *Cocconema*, and therefore of the allied genera, is developed from the frustules, is well-shown in a curious state of *Cocconema lanceolatum* which I have recently found. In this, each pair of frustules, instead of being raised upon a long stalk, has become invested with a definite mucous or gelatinous envelope of the same character as the short stipes to which it is attached, and of which organ it would appear to be an abnormal condition. In *Schizonema* the gelatinous sheath may often be shown to bear a proportion to the number of frustules it contains. In a freshwater species of *Schizonema*, occurring abundantly in the neighbourhood of Bristol, the common mucous sheath is liable to considerable modification according to the circumstances under which the plant grows. It occurs in some situations in the form of a mucous stratum upon the surface of stones; in others the gelatinous sheath is of extreme tenuity and transparency: whereas, if the plant is found in rather deep rapid streams, the sheath is much-developed and becomes of an almost membranous texture; thus showing that this gelatinous structure is of subordinate character, and may vary according to the circumstances in which the plant is found.

Microcoleus possesses a gelatinous sheath, but in the allied genera *Oscillatoria*, *Calothrix*, &c. this is represented by a truly membranous sheath, closely resembling and no doubt identical in function with cell-membrane. This fact, coupled with what is observed during the formation of the spore of *Zygnema*, where the endochrome seems at first to be held together by mucus, would make it appear not unlikely that cell-membrane is really a modification of a similar mucus or gelatine, and that the ultimate structure of both is similar.

In examining the fronds of some of the foliaceous Algæ, it may very readily be perceived that the cells composing it are separated from one another by the interposition of an apparently homo-

geneous gelatinous structure called the intercellular substance. This substance is no doubt analogous to the mucus of the *Palmelleæ*, and of similar character to it. That this is the fact may be well-seen in attending to the mode of development of the frond of *Tetraspora*, in which a quaternary division of the cells takes place, as in some species of *Palmelleæ*: around each of the new cells, though principally on one side of them, is developed a definite amount of gelatine; and in this way the size of the frond is increased. This genus, *Tetraspora*, forms a beautiful connecting link between the *Palmelleæ* and the laminose Algæ; for although the mass of cells is developed in the form of a frond, still these cells have their individual development but slightly modified by forming a part of an entire structure. In some *Ulva* the character of a whole compound structure is more manifest, and the individual cell-life begins to appear secondary; and as we advance higher in the scale of vegetation, the latter ceases to speak plainly to our senses.

If what I have said respecting the intercellular structure is true of the Algæ, the same explanation would apply to that structure in the higher plants, where it is often very conspicuous; and it appears to me not improbable, that the deposits of sclérogen as well as the firm portion of the spiral fibre may be considered as structures of a similar character. The pellicle which covers the cuticle is doubtless so.

Now what is the character of the mucus which we have seen to be developed in definite quantity outside and around the cell-wall? That it is not a mere chemical solution of starch would appear evident from its persistence when mounted for the microscope in water and other fluids. Its toughness and elasticity, the readiness with which it allows water to permeate it, and its recovering its original form and consistence upon being moistened after desiccation, seem to warrant the belief that it possesses an organized form of the same mechanical properties as sponge; and if we could resolve it under the microscope into its ultimate structure, we should probably find that its texture would be best expressed by the term *spongy*; though I would not wish it to be supposed I believe it to have the complicated structure of real sponge, but to consist rather of a mat of delicate fibres.

And as, in viewing a series of Algæ, a transition may be observed from a mucous structure to one possessing the external characters if not the functions of cell-membrane; it may be fairly inferred that cell-membrane is of a very similar mechanical structure, and we should perhaps not be far from a right definition in applying to it the term *felt*, as indicating its real characters.

After duly weighing the foregoing phænomena and others of a similar character, I have arrived at the conviction that the cell-

membrane is quite a subordinate part of the living structure; that its functions are of a purely physical character; that its principal office is to protect, locate or isolate the matter it contains; and that any vitality it possesses is derived from the presence within it of its endochrome. There are, however, a few phenomena which at first sight would appear to militate against the opinion I have advanced; I mean the contractility of certain membranes, and the movement of ciliary appendages belonging to others. It is very certain, that during the vital processes which are going on in the interior of the cell, considerable chemical changes are taking place; and these must of necessity give rise to an elimination of electrical currents. The presence of such currents would, I think, be sufficient to account for the rhythmical movement of cilia, as well as for the contraction of membranes of certain mechanical structure.

I would ask whether these electrical currents may not give rise to the formation of the mucus surrounding the cell, and determine its character and extent; whether, too, the production of cell-membrane may not occur under a similar influence; and whether this would not be the easiest solution of the problem of how the cell is increased in size? viz. that a formation of cell-membrane takes place within the range of these currents, whilst absorption occurs within or without it. On this principle, too, we can better understand the process of the fissiparous division of cells; the endochrome becoming divided into two portions, two centres of electrical force are originated, and each of these giving rise to a set of currents, two cell-membranes are produced instead of the original one. The frequent occurrence of nests of regular crystals (not sand) in the substance of the mucous envelopes of such freshwater genera as *Batrachospermum*, *Chatophora* and *Monormia*, would seem to afford positive proof that electrical currents exist there.

These views, if correct, would of course apply to animal as well as vegetable organisms, and we should be under the necessity of considering the entire membranous or solid portion of the animal as of a subordinate character to the fluids contained in its cells, and merely as an instrument acting in prompt obedience and conformity to the changes taking place in these fluids.

But treating the subject of the functions of the cell-membrane in a chemical point of view, we know that considerable chemical changes are taking place during the processes of assimilation, secretion, elaboration, &c.; that these are essentially chemical phenomena. Are we to look to an organ of such a low chemical constitution as cell-membrane as likely to give origin or the initiative to these important changes? I cannot believe such can be the fact, but that the organ or substance which gives

